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A NEW SPECIES OF VICTORELLA FROM SOUTHERN CALIFORNIA (BRYOZOA: CTENOSTOMATA)[1]

By WILLIAM C. BANTA[2]

A new species of ctenostome polyzoan, *Victorella argilla*, has been discovered in great abundance in seven southern California locations. It exists in two growth forms, similar to the growth forms of *Victorella pavida* Kent. In the younger stage (form A) the animal is nearly indistinguishable from certain species of *Arachnidium*, whereas the older stage (form B) shows closer affinities to *Nolella* and *Cryptopolyzoon*. In many respects, especially the budding of new zooids from the apertural papilla, the animal is a typical *Victorella*. In others, however, it is unique: it inhabits marine waters, not brackish ones as do other *Victorellas*, and it possesses peculiar filiform processes modified for the accumulation of sediment.

The colony consists of more than one-half inorganic matter tightly bound to the zoecia by an adhesive. The spreading zoaria appear early in the pattern of ecological succession of some environments and effectively crowd out many competitors. It is the most abundant animal species in certain areas.

This paper would not have been written without the patient efforts of Robert R. Given, to whom credit should be given not only for the

[1] Contribution no. 289 of the Allan Hancock Foundation.

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discovery of *Victorella argilla* but also for much of the ground work necessary for its characterization. I especially wish to thank Patricia L. Cook of the British Museum (Natural History) for her helpful advice and criticism and for the loan of a number of specimens, John S. Bullivant for his invaluable suggestions, and John D. Soule for his kind encouragement and loan of specimens. G. Dallas Hanna, William Miller, D. W. Kelley, and J. S. Ryland were of great help in locating material; K. June Lindstedt and Kristian Fauchald deserve special mention for their help in illustrating, translating, and otherwise readying the manuscript for press. Many thanks also are due Russel L. Zimmer, Olga Hartman, John L. Mohr, Diane Robbins, Robert Woollacott, and Timothy Wyatt for their critical readings of the manuscript.

Victorella Kent, 1870

Victorella argilla, new species

Holotype.—United States National Museum, Washington, D.C., USNM no. 11918: fragment of form A colony fixed in Bouin's fluid and preserved in 70 percent alcohol.

Paratypes.—USNM no. 11919: fragment of form B colony fixed in Bouin's fluid, preserved in alcohol. Allan Hancock Foundation, University of Southern California, Los Angeles; colonial fragments, form B. Some additional paratype material is retained in the author's collection. All material is from the type-locality (see p. 10).

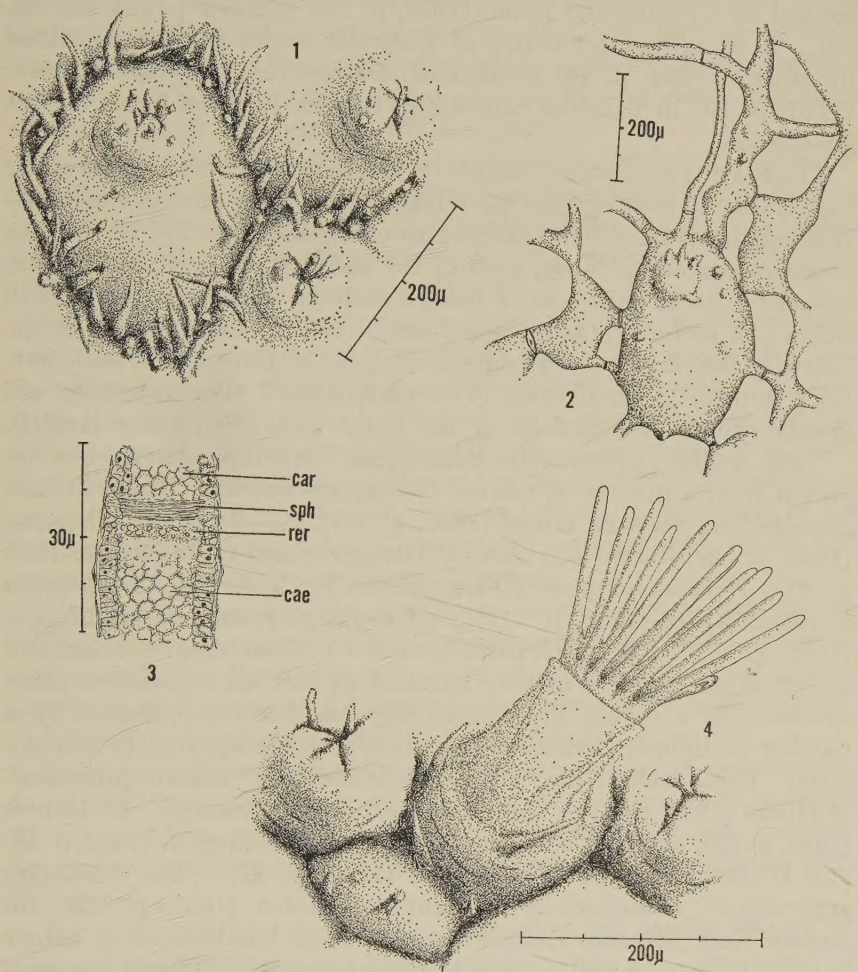
Diagnosis.—Young colonies (form A) are composed of flattened zoecia connected by septate tubular evaginations of the body wall, which anastomose irregularly, producing an *Arachnidium*-like colony. Older zoecia (form B) are produced by a pronounced elongation of the apertural papilla, drawing the polypide away into the tubular portion of the zoecium.

The zoecia bear numerous filiform processes modified for the accumulation of foreign material, and old zoaria form thick, tough layers with a very high content of inorganic matter, especially silt. The polypide has 12 tentacles; an intertentacular organ is present in form B. There is no gizzard, a single funiculus; vestibular muscles are bilateral (form A) or radial (form B), and the aperture is not quadrangular.

Form A

Zoarium.—In this growth form the species is a thin unilaminar mat of flattened zoecia resembling a small *Alcyonidium*. The zoecia, where clearly seen, are brownish to colorless, oval, and measure 0.3–0.4 mm long by 0.2–0.3 mm wide. In the center of the colony the zoecia stand in close quincunx (fig. 1), communicating with one

another through very short tubules that originate from the basal-lateral wall of the zoecium. In the more peripheral portions of the colony the tubules are considerably longer and the zoecia are wider apart (fig. 2).



FIGURES 1–4.—*Victorella argilla:* 1, three zoecia from the center of a form A colony; 2, developing zooids and anastomosing tubules from the periphery of a form A colony; 3, tangential section at the junction of the cardium and caecum of a form A zooid (see fig. 7: sph.) (abbreviations: cae=caecum, car=cardium, rer=reinforced region, sph=sphincter); 4, surface of a form B colony, one polypide extruded.

Intercalary tubules are interrupted by a thick septum with a heavily reinforced annulus and a small central pore. There is only one septum per tubule; the tubules are therefore not kenozoecia and do not represent true stolons in the sense of Silén (1944, p. 29).

New zooids are formed at the periphery of the colony by the anastomosis of thin-walled tubules that originate as simple evaginations from the basal-lateral wall of young zoecia. The method is reminiscent of the budding pattern of *Arachnidium fibrosum* Hinks as described by Prenant and Bobin (1956, p. 228; see also p. 224 and fig. 99). It is unlike the budding of *Victorella pavida* Kent as described by Braem (1951, p. 10) or that of *Arachnidium irregulare* Harmer (1915, p. 49) in that the connecting tubules of these forms do not anastomose.

Filiform processes.—Early in development, even before the first traces of the polypide have begun to appear, elongate evaginations originate on the frontal surface of the zoecium (fig. 2). These processes are conspicuous, even at the early stage shown in figure 2, because a thick, dark coat of foreign material is already adherent to them. In section these processes can be seen to be composed of the following four layers: (1) an outermost layer of detritus and sediment; (2) a cuticle; (3) epidermis; (4) a peritoneum. The processes are clearly simple evaginations of the body wall. Septa are lacking.

Very similar, presumably homologous structures have been reported from a number of related ctenostome species. These include *Arachnidium fibrosum* Hinks (1880, p. 511), *Nolella sawayai* Marcus (1938, p. 52), *Nolella horridum* (O'Donoghue and O'Donoghue, 1926 p. 61), *Nolella spinifera* (O'Donoghue, 1942, p. 59), *Arachnoidea barentsia* Kluge (1962, p. 212), and *Cryptopolyzoon evelinae* Marcus (1942, p. 477). The structures have not been studied in detail and each author has coined his own terminology without reference to other species. As a result, the terminology has become cluttered by a number of different terms for structures that are apparently homologous. These include the "lateral processes" and "filiform processes" of Hinks (1880, p. 511), the "free encrusted appendages" of Marcus (1938, p. 52), and the "spinous processes" of O'Donoghue (1924, p. 59) and O'Donoghue and O'Donoghue (1926, p. 21). The "cuticular appendages" described by Prenant and Bobin (1956, p. 227) for *Arachnidium fibrosum* include broader basal lobations that adhere to the substrate, as well as erect, elongate processes. The structures of *Cryptopolyzoon evelinae* called "adhesive papillae" by Marcus (1942, p. 478) apparently include not only homologous elongations but some true kenozoecia as well. The term "filiform process" seems the most appropriate and is the name that will be used here for any filiform, aseptate evaginations of the body wall.

The filiform processes of *Victorella argilla* are modified for the accumulation of foreign material and secrete large quantities of an adhesive substance that stains a bright turquoise in Alcian Blue

(suggesting an acid muco-polysaccharide). They are most abundantly developed on the marginal portion of the frontal surface or in the vicinity of the apertural papilla (fig. 1), but they may occur on the connecting tubules as well. In some cases, filiform processes are produced on the wall of the vestibule near the aperture so that, when the lophophore is withdrawn into the zoecium, the detritus accumulated on the neck of the extruded polypide is drawn directly into the vestibule. Vestibular filiform processes can be seen protruding from the apertures of the zoecia shown in figure 1.

Digestive system.—The digestive system of form A is illustrated in figures 3, 5, 6, and 7. The lophophore, when retracted, is oriented parallel to the surface and at right angles to the vestibule, which is situated directly below the aperture (fig. 7). There are 11, 12, or 13 tentacles, 12 being the more common.

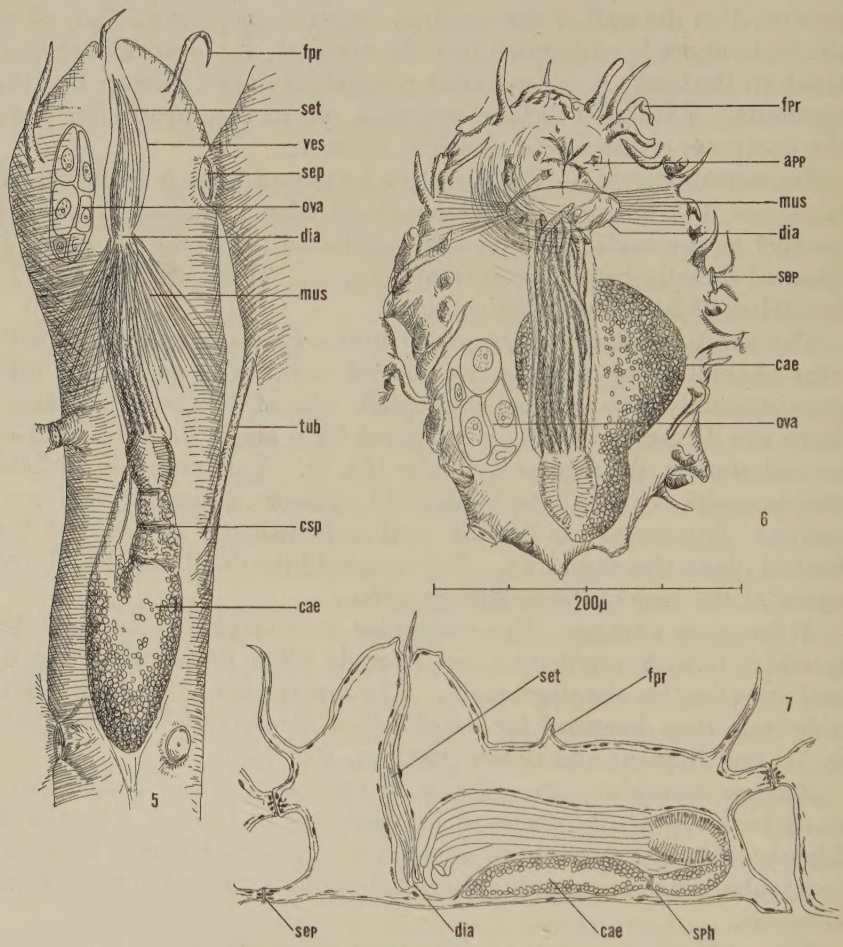
The short, ciliated pharyx passes into a spacious esophagus with very characteristic elongate, vacuolated cells. The esophageal cells pass insensibly into rounded eosinophilic cells of the cardiac stomach. Here the digestive tract is interrupted by a single discrete band of smooth muscle, the cardiac sphincter (fig. 3). The sphincter, without visible nuclei, is immediately followed by a short, ill-defined reinforced region. The caecum is broadly oval and distinctly flattened in the frontal plane (fig. 6 and 7). The rounded intestine leads distad and opens at the base of the setigerous collar.

Muscular system.—The vestibular musculature is strongly bilateral in form A, originating distolaterally below the vestibule (fig. 6) and inserting on the diaphragm. The arrangement is indistinguishable from that described for *Arachnidium fibrosum* by Marcus (1938, p. 51) and Prenant and Bobin (1956, pp. 227–228).

Reproductive system.—Testes in various stages of development have been repeatedly observed in specimens of form A collected in March 1965, but ovaries are uncommon. I have not seen an intertentacular organ in a zooid of form A, but one is present in many form B zooids.

The apertural papilla.—The term apertural papilla follows the usage of Silén (1944, p. 26) and is equivalent to the "peristome" of Ryland (1958, p. 317), the "tubular peristome" of Prenant and Bobin (1956, p. 233), and the "upright cylindrical structure" of O'Donoghue (1924, p. 59). In the typical form A zoecium, the apertural papilla is low, rounded, and occupies only about a third of the length of the zoecium (fig. 1). Transition from the A to the B form occurs through the exaggeration of the apertural papilla and the assumption of vertical budding of new zooids from the upright portion of the zoecial wall. Although they may be distinguished readily in their extreme forms,

there is no clear line of demarcation between the A and B forms. Both forms occur on different regions of the same colony with a region of transition between them.



FIGURES 5–7.—*Victorella argilla*, schematic drawings (parietal muscles, retractor muscles, and testes omitted): 5, distal end of a form B zooid; 6, form A zooid, frontal view; 7, schematic median saggital section of a form A zooid. (Abbreviations: app=apertural papilla, cae=caecum, csp=central sphincter of three, dia=diaphragm, fpr=filiform process, mus=apertural muscles, ova=ovary, sep=septum, set=setigerous collar, sph=sphincter muscle of form A, tub=connecting tubule.)

FORM B

ZOARIUM.—Foreign material in the form of siliceous sediment and detritus is extensively integrated into the mature colony of form B. The relative quantity of nonoxidizable inorganic material can be

estimated by weighing portions before and after drying to constant weight (at 60° C) and again after digestion of the colony in boiling sodium hypochlorite. The results are as follows:

constituent	*percent by weight*
non-oxidizable material	49.1
water	45.4
dry organic matter	5.5
	100.0

The large quantity of foreign material frustrates interpretation of zoarial structure. Attempts to separate the animals physically from the sediment have met with failure. Perhaps the most satisfactory method, suggested by Patricia L. Cook of the British Museum (Natural History), is to shake the material in 10 percent trisodium phosphate.

Attempts to cultivate the animal in the presence and absence of suspended calcareous material (finely ground aragonite), have failed, due probably to starvation, although the animals were offered a variety of diatoms and dinoflagellates at varying concentrations while they were being maintained at different temperatures (10°, 15°, and 20° C).

Because of the difficulty in isolating *Victorella argilla* from its investment of foreign material, most of the conclusions about the zoarial structure of form B have been drawn from very thick paraffin sections, despite their poor technical quality. Only the examination of a great number of serial sections has made an accurate interpretation possible.

The zoecia of the mature form B are exceedingly elongate, without a basal dilation, and oriented perpendicular to the substrate. They are closely packed so that only the rounded tips of the apertural papillae and their filiform processes are visible at the surface (fig. 4). Mature zoecia are so variable in length and the sections are so distorted, it is impossible to estimate an average length, but the largest zoecia are very long and reach deeply into the thick zoarium. It is at least likely that some of the zoecia reach all the way to the substrate, suggesting that the zoecia must be among the largest of the Polyzoa—more than a centimeter in length. The polypides, however, are much shorter (0.3 mm) and are restricted to the most superficial parts of the colony. New zooids, which differ from adults only in length, are produced near the zoarial surface from the lateral wall of the mother zooid. In a few cases, they are produced, as in form A, by the dilation of connecting tubules, but the morphology is always that of form B. Form A zooids may give rise to form B zooids, but the converse apparently is not true.

The basal part of the zoarium is a poorly organized mass of zoecial tubes and degenerated "stolons." In some regions the zoecia are

obviously dead, so that the basal parts of the thickest carpets are probably formed from collapsed and degenerating zoecia and connecting tubules held together by the adhesive substance secreted by the filiform processes. Septa are more resistant than the rest of the zoecium and are quite conspicuous in fuchsin-stained material as loose red discs with a central perforation. Brown bodies are distributed irregularly through the tubular zoecia, indicating that the animals grow by the successive death and replacement of several polypides in the same zoecium. The space between zoecia is filled with dense masses of detritus and sediment tightly cemented into the colony by the remains of filiform processes and probably also by an adhesive material produced on the cuticle itself. Filiform processes are represented more sparsely on the zoecial walls than on the exposed tips of the zoecia. It seems likely that they are formed at the growing tips and break down as the zoecium elongates distally (figs. 4, 5).

Muscular system.—Because the zoecia are tubular and because the polypides are confined to the most distal portion of the upright cystid, the tentacle sheath and vestibule are directly in line with one another and the strong bilateral symmetry of the apertural muscles seen in form A has been lost. The strong vestibular muscles probably are associated with the habit of drawing foreign material into the vestibule. Both the vestibular wall and the orificial collar are exceedingly sticky and large masses of foreign material, including sand grains nearly as large as the diameter of the zoecium, are introverted when the lophophore is retracted. As a result, the vestibules of all zoecia old enough to feed are packed solidly with foreign material. It has not been possible to ascertain how this material is eliminated when the polypides degenerate, but none has been observed incorporated into brown bodies.

The apertural muscles of form B arrange themselves radially around the vestibule and show none of the bilaterality of form A (see p. 5).

In some species (e.g., *Victorella pavida*), the disposition of the apertural muscles into four evenly spaced clusters imparts a quadrangular shape to the closed aperture. Even the apertures of tightly retracted zooids of *Victorella argilla* are puckered irregularly. It should be noted that all other species of *Victorella* so far described possess quadrate apertures (Braem, 1951).

Digestive system.—Braem (1951, p. 23) attaches considerable taxonomic importance to the location of the sphincter muscle of the cardiac stomach. One of the principal reasons he gives for separating the genus *Tanganella* from *Victorella* is that the sphincter muscle of the latter is placed near the middle of the cardiac stomach while, in

the former, it is at the junction of the cardium and the caecum. Unfortunately, it is difficult to delimit the cardiac stomach in *Victorella argilla* because a cardiac valve is lacking in this species. Nevertheless, it is clear that the greater part of the distal digestive tract proximal to the vacuolated cells of the esophagus is invested in very fine concentric muscles that may become elaborated into well-defined sphincter muscles at three possible sites. Figure 5 shows a polyp with all three sphincters developed though, as a rule, only one or two bands are present at a time. There is no trace of a gizzard or other chitinous reinforcement of the distal digestive tract.

Reproductive system.—Both form A and form B individuals have been found to contain ripe testes and ovaries. Both gonads occur in the distal region of the zoecium of form B, but they are located more proximally in form A. An intertentacular organ is present in most of the form B individuals examined, but I have not observed any in form A.

One of Braem's (1951, p. 33) reasons for separating *Tanganella* from *Victorella* was the possession of an intertentacular organ by the latter (*Victorella*) but not by the former (*Tanganella*). Sexually mature *Tanganella* extrude their eggs through a supraneural pore (Braem, 1951, p. 27; see also his discussion of *T. mulleri* on p. 6).

Unfortunately, none of the material at my disposal contains embryos and there is no sign of a modification of the vestibular wall to indicate that brooding takes place there as it does in *Tanganella mulleri* (Braem, 1951, p. 27). The extensive mass of foreign material filling the vestibule indicates that if indeed eggs are brooded in this species, the brooding must almost certainly take place elsewhere—in the tentacle sheath, for example.

Ecology

The mature colony of form B is typically a thick, sandy or argillaceous carpet growing in sheets or knobs over hard substrate. The well-developed colony is by no means easily recognized as a polyzoan because of the massive accumulation of detritus and sediment between the zoecia. When the lophophores are retracted, foreign material effectively obscures the apertures, so that, even under high magnification, the colony is easily disregarded as inorganic. Teasing apart the zoarium fails to yield any information because the zoecia and connecting tubules form a tightly integrated mass, and zoecia tend to tear open rather than separate, with the result that the fragile polypides are lost against a background of sediment.

Victorella argilla, nevertheless, is quite abundant. It has been recorded from seven localities from Tomales Bay to Imperial Beach

Calif.; at each place it is present in great abundance. At the type-locality (Hermosa Beach, Calif.), for instance, virtually every exposed surface of the rocky environment is covered with a dense mat of *Victorella argilla* several centimeters thick.

Turner, Ebert, and Given (in ms.) have described the ecology of artificial reef environments and have recorded the impact of *Victorella argilla* on biological succession. These authors found that hard surfaces exposed to waters containing large amounts of suspended sediment were colonized by *V. argilla* at an early stage in the successional pattern. The animal becomes a thick, rapidly spreading mat that smothers and kills other sessile animals and inhibits the settling of competitors by the dense, muddy surface it presents. At length, the colony thickens, rising up into smooth knobs and clumps. These thick masses break away easily and apparently the surfaces thereby exposed are among the few places other animals may become attached. These authors report that the colony had been noticed but not recognized as organic until late in the study. It was referred to as a sediment layer or a muddy mucous layer until its animal nature was discovered by Given.

The following is a list of the Polyzoa from the type-locality:

Victorella argilla, new species	abundant
Pherusella, undescribed species	present
Tubulipora tuba Gabb and Horn, 1862	present
Diaperoecia californica (d'Orbigny, 1852)	abundant
Diaperoecia floridana Osburn, 1940	common
Crisia occidentalis Trask, 1857	common
Membranipora villosa Hinks, 1880	on algae
Antropora tincta (Hastings, 1930)	on *Kelettia*
Scrupocellaria bertholetti Robertson, 1905	common
Microporella californica Robertson, 1908	present
Fenestrulina malusi (Audouin, 1826)	present
Holoporella brunnea (Hinks, 1884)	present

Distribution

Type-locality.—California Wildlife Conservation Board, cement block artificial reef, Hermosa Beach, Calif., 60 feet. Type material collected by the author June 10, 1965.

Mr. Robert Given informs me he has observed the animal at the following locations: Malibu artificial reef, Malibu, Calif., 60 feet (May 8, 1961); Standard-Humble oil tower "Hilda," Santa Barbara, Calif., from 10 to more than 110 feet (1961); artificial reef at Torrey Pines, near La Jolla, Calif., 65 feet (Oct. 19, 1964); docks and piers at the University of California at La Jolla; artificial reef at Imperial Beach, Calif., 15–20 feet (Oct. 20, 1965); artificial reef at Huntington Beach, Calif., 65 feet (Oct. 22, 1964).

I have examined specimens of the animal identified as *Alcyonidium parasiticum* (Fleming, 1828) by Soule (1953, p. 729). The specimens are almost certainly identical with form A of *Victorella argilla*, which extends the range of the species to Tomales Bay, Calif., 30 feet; Dr. Raymond C. Osburn, collector.

Discussion

The genus *Victorella* has been reviewed in detail by a number of zoologists (Annandale, 1911; Braem, 1951; Brattström, 1954; Marcus, 1925, 1940; Soule, 1957; and Valkanov, 1943). The most complete summary is that of Brattström (1954), wherein he reviews the tangled and controversial taxonomy of the genus but finally is able to conclude, with Valkanov (1943, p. 4), only that "we are a long way from a correct view of the genus *Victorella*."

Most of the taxonomic trouble stems from a long-standing controversy over whether or not *Victorella mülleri* Kraepelin, 1897, and *Victorella pavida* Kent, 1870, are the same species. As Brattström (1954, p. 8) points out, *V. mülleri* has never been taken from waters in which *V. pavida* does not occur. Some authors, led by Valkanov (1943), Marcus (1940), and Soule (1957), are of the opinion that *V. mülleri* is only a "growth phase encountered in the younger colonies of *V. pavida*" (Soule, 1957, p. 25) and point to the wide variability of the characters used to separate them. Braem (1951, p. 22), on the other hand, not only is of the opinion that they are distinct species, but also maintains that the differences are so fundamental that the species must be relegated to separate genera. After perhaps the most exhaustive recent study on the genus, Braem (1951, p. 33) concurs with previous authors that such characters as the relative length of the upright portion of the zoecium and the number of folds in the setigerous collar are of only superficial value in separating species or genera. He concludes, nevertheless, that *V. pavida* and *V. mülleri* may be distinguished on the basis of the following characters: (1) the cardiac sphincter in *V. pavida* is developed at the center of the cardiac stomach, whereas it is at the proximal end in *V. mülleri*; (2) an intertentacular organ is present in *V. pavida* but is replaced in *V. mülleri* by a supraneural pore at a corresponding position; (3) the embryos are brooded in the vestibule of *V. mülleri*, but the reproductive habits of *V. pavida* are not fully known (Braem, 1951, p. 33). Soule (pers. comm.) has pointed out that he misquotes Braem in his (Soule's) 1957 paper (p. 25). He states that entirely different characters were used in the generic description of *Tanganella* by Braem (1951, p. 33).

Other characteristics, such as the length of the apertural papilla and the pattern of budding, are useful, but wide variability makes

them unreliable. The danger of employing these superficial characters is multiplied further by the existence of animals essentially indistinguishable from *V. pavida* but closely approaching *V. mülleri* in some respects. Braem (1951, p. 45) has erected a new species and genus, *Bulbella abscondita,* to include them. The species occurs only where both *V. pavida* and *V. mülleri* are common.

With regard to item 1 above, Braem (1951, p. 23) himself points out that the position of the "sitzenden Sphinkter" [fixed sphincter] is the most "wesentlich und konstant" [fundamental and constant] feature distinguishing *Victorella* from *Tanganella,* yet he states: "Die Lage des sitzenden Sphinkter ist nicht immer ganz gleich, da die benachbarten Darmteile einigermasser gegeneinander verschiebar sind" [The position of the fixed sphincter is not always entirely the same since the neighboring parts of the gut are somewhat displaceable against one another] (loc. cit.). A glance at his figures (plate II: fig. 9 and plate V: fig. 5C) is enough to convince a reader that the overlap is considerable. The situation in *V. argilla,* with its diffuse system of muscle bands around the entire distal portion of the gut, appears to cast doubt on the validity of this character among ctenostomes; nevertheless, if characters of this nature should prove reliable, then the position of the sphincter in form A of *V. argilla* would seem to ally it more to *V. pavida* (and *Bulbella abscondita?*) than to *V.* (=*Tanganella*) *mülleri.*

As regards items 2 and 3 above, *V. argilla* further resembles *V. pavida* in the possession of an intertentacular organ (lacking in *V. mülleri*). Unfortunately, little is known of the reproductive habits of *V. argilla* (see p. 9).

It is obvious that the systematics of *Victorella* and its relatives is unstable and that much of the confusion has arisen from an uncertainty as to what characters are of importance. Since it is not at all clear what the limits of the genera (or even of the species) should be, I am exceedingly hesitant to further confound the already perplexing taxonomy by inserting yet another genus into the literature. Therefore, even though the differences between *V. argilla* and other *Victorella* are greater than those between most other genera in its family (between *Victorella* and *Sundanella* or *Bulbella* and *Tanganella,* e.g.), I place it in the genus *Victorella* as defined by Prenant and Bobin (1956, p. 139). It should be distinguished from all other members of the genus by the following characters: (1) the possession of filiform processes that secrete an adhesive that causes them to be invested in a coat of foreign material; (2) the disposition of the apertural muscles into a radial or bilaterally paired configuration (the aperature of the retracted zooid is therefore not quadrangular); (3) the marine habitat of *V. argilla.* All other described forms are known only from brackish

waters. The marine species *V. sibogae* Harmer (1915) has been removed by Braem (1939, p. 178) to a new genus, *Sundanella*, on anatomical grounds; Marcus (1941) agrees. The other morphological characters of specific value depend on whether or not the animal is in the A or B form.

A number of explanations have been given for the great variations of zoecial form in *Victorella*. In general, those authors who consider *V. mülleri* synonymous with *V. pavida* have offered two explanations for variation in zoecial length: the age of the zoecium and crowding of the colony. Most of these authors (Ulrich, 1926; Annandale, 1912; Borg, 1930; Braem, 1911; Soule, 1957; and Carrada and Sacchi, 1964) are of the opinion the *V. mülleri* is a juvenile form of *V. pavida*. The best presentation is that of Ulrich (1926). Valkanov (1943, p. 5), on the other hand, seems convinced that zoecial crowding caused by local irregularities of the substrate induces a lengthening of the zoecium, presumably by restricting growth laterally. More recently Brattström (1954, p. 11) stated: "It is possible that the two species here treated (if really separate) are capable of great seasonal variations as well as of variations resulting from environmental influences (temperature, density of colonies, etc.) and thus, though anatomically different, being able to appear in different growth forms which are more or less alike in the two species."

In the case of *V. argilla*, the elongate B zooids are produced in two possible ways: (1) by the elongation of the apertural papilla vertically from the substrate and the degeneration of several successive polypides, as described on page 8 (in this case, it is true that variability is age-induced and that A colonies invariably produce B colonies, but it should be noted that the zoecial wall of the B form represents the apertural papilla of the A form); (2) by the budding of B zooids. As mentioned before (p. 7), new buds may be formed as evaginations of the body wall of the upright portion of the zoecium; such buds produce only B zooids. Conversely, however, only A zooids are ever produced by the "stolonal" budding of another A zooid (see p. 7). This peculiar state of affairs may represent some biochemical difference in the two kinds of buds but it could as easily be due to some more direct physical influences. The zoecia may be so crowded, for instance, that only vertical growth is possible, or perhaps the volume of B zooids is too great for the quantity of foodstuffs that can be transmitted to the bud from feeding autozoecia through the connecting tubules. In this case, perhaps only the efforts of several generations of polypides within the same zoecium is enough to provide the nourishment necessary to produce the large B zooids. It should be recalled that some of these zooids may approach a centimeter in length (see p. 7).

The variations encountered in the two growth forms of *V. argilla* are far more fundamental, however, than mere changes in the shape and form of the zoecium. There are extensive changes, for instance, in the morphology of the digestive tract, muscular system, and reproductive system. Many of these changes are related to, if not a direct consequence of, the differences in zoecial shape. The basal-frontal flattening of the stomach in form A is almost certainly a consequence of the flattened shape of the zoecium to which it is confined. The same is probably also true of the differences in arrangement of the apertural muscles; the shape of the form A zoecium makes a bilateral arrangement of the muscles around the vestibule a virtual necessity (fig. 6). Other morphological changes are explained less readily. It is difficult to see a relationship, for instance, between the disposition of sphincter muscles around the cardinal stomach, on the one hand, and the degree of flattening of the stomach or the relative length of the zoecium, on the other. There is clearly a need for more exhaustive research before it will be possible even to propose a reasonable theory of the causes of variability.

Whereas the closest affinities of *V. argilla* appear to be with the other members of its genus, there are clear indications of relationships to other genera. Form A of *V. argilla* is almost indistinguishable from the not uncommon temperate ctenostome *Arachnidium fibrosum* Hinks 1880. They are alike in the possession, distribution, and function of filiform processes, the manner of growth (i.e., by the extension, dilation, and anastomosis of tubules), the structure of the apertural muscles, the absence of a gizzard, and the size and shape of the zoecium. In short, a specialist would be hard put to distinguish the two animals were it not for the somewhat denser manner of growth of *V. argilla* and its gradual extension into the B form. It should be noted, however, that *A. fibrosum* differs from other members of its genus in a number of respects. It possesses filiform processes and the pattern of budding differs somewhat from that of other species of *Arachnidium* (Prenant and Bobin, 1956, pp. 223–228).

Arachnidium fibrosum (and form A of *V. argilla*) might be mistaken easily for certain species of the genus *Nolella*, particularly *N. sawayai* Marcus (1938, p. 52), a peculiar species possessing filiform processes but having a long apertural papilla. The close relationship between *Nolella* and *Arachnidium* has been noted by Rogick (1949, p. 165), Harmer (1915, p. 58), Ryland (1958, p. 31), and others. Rogick, for example, only hesitantly refers her new species *N. blakei* to the genus *Nolella*, noting (1949, p. 165) that some individuals with very short apertures are better ascribed to *Arachnidium*. Other zoecia are clearly transitional.

Nolella, moreover, shows clear relationships to *Victorella*. Some

authors (Prenant and Bobin, 1956, p. 239; Soule, 1957, p. 28) have commented on the similarities between the genera. In fact, there seem to be only two criteria for distinguishing them: (1) the fresh or brackish water environment of *Victorella* (except *V. argilla*); (2) the occurrence of zoecial budding from the apertural papilla in *Victorella* but not in *Nolella*. As Braem (1951, 11) has pointed out, however, young colonies of *V. pavida* do not show budding of this sort. The close relationship between *Nolella* and *Victorella* was emphasized by Soule (1957, p. 28), who places *Victorella* in the Nolellidae. This classification will be followed here, but it should be noted that this scheme does not indicate the close relationship between the Nolellidae and the Arachnidiidae. The family Nolellidae was placed in the Division Stolonifera by Soule (1957, p. 27–28) on the basis of the order of development of the apertural, parietal, and retractor muscles. As hinted by Ryland (1958, p. 317), this makes the family the only member of the Stolonifera to lack true stolons as defined by Silén (1944, p. 28). *Nolella* apparently lacks true stolons (Soule, 1953, p. 737; Rogick, 1949, p. 159) and *Victorella* almost certainly does (Braem, 1951, pp. 10–12).

In addition, *V. argilla* shows some links to *Cryptopolyzoon evelinae* Marcus, 1942. Both are similarly committed to the incorporation of foreign material, and both possess filiform processes, especially near the aperture (Marcus, 1942, p. 478). *Cryptopolyzoon* differs, however, in the possession of a true gizzard (Dendy, 1888, pp. 6–7, pl. II: fig. 8), a quadrangular aperture, the erect, dichotomously branching growth habit, and other aspects.

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